NOTES ON THE MORPHOLOGY AND BIOLOGY OF *CTENOPHORUS McKENZIEI* (STORR, 1981) (SQUAMATA: AGAMIDAE)

by M. PETERSON*, G. M. SHEA†, G. R. JOHNSTON‡ & B. MILLER§

Summary

PETERSON, M., SHEA, G. M., JOHNSTON, G. R., & MILLER, B. (1994) Notes on the morphology and biology of *Ctenophorus mckenziei* (Storr, 1981) (Squamata: Agamidae). *Trans. R. Soc. S. Aust.* 118(4), 237-244, November, 1994.

The systematic status of *Ctenophorus mckenziei* is reviewed, on the basis of additional material from Western Australia and South Australia. Habitat data for known localities, stomach contents, one record of clutch size, and behavioural observations and thermal preferences of captive individuals are provided. *C. mckenziei* is morphologically very similar to *C. scutulatus*, differing mainly in adult size and subtle modifications of colour pattern. *C. mckenziei* and *C. scutulatus* are phenetically most similar to *C. cristatus*.

KEY WORDS: Squamata, Agamidae, *Ctenophorus*, morphology, biology, habitat, diet, thermal biology.

Introduction

The agamid *Amphibolurus mckenziei* was described from two specimens (Western Australian Museum [WAM] R59753-54), collected at 5 km and 8 km SW of Ponier Rock, Western Australia (Storr 1981). The species was subsequently transferred, with a number of other agamid species, to *Ctenophorus* (Storr 1982). Additional specimens of *C. mckenziei* have since been reported from Western Australia and South Australia by Schwaner & Tyler (1985), McKenzie *et al.* (1987), Anon. (1988), Wilson & Knowles (1988), Armstrong (1992) and Ehmann (1992). This additional material, previously uncharacterised, considerably extends our knowledge of the morphology, distribution and habitat preferences for this species and provided the basis for this paper.

Materials and Methods

Five specimens from Western Australia, additional to the types, have been collected: South Australian Museum (SAM) R2832, Western Australia; WAM R91764-65, 9 km E Kilidwerinia Granite Rock, 32°04'S 124°00'E, 29.iii.1984; WAM R91842, R91852, 15 km E Kilidwerinia Granite Rock, 32°03'S 124°05'E, 5.x.1984. Eleven specimens have been collected from South Australia: SAM R25572, R26162, 12.6 km (air distance) NE "Colona", 31°31'S 132°09'E; SAM R26160-61, 16.2 km (air distance) NE "Colona", 31°31'S 132°11'E; SAM R26890, 15.2 km (road

distance) NE "Colona", 31°31'S 132°09'E, 13.xi.1984; SAM R32264-65, R32268-69, 0.5 km S Mitcherie Rockhole, Yumburra Conservation Park, 31°27'S 132°49'E, 17.x.1987; SAM R32266-67, 5 km S Mitcherie Rockhole, Yumburra Conservation Park, 31°29'S 132°50'E, 18.x.1987 (Fig. 1).

Measurements taken on preserved material follow those used by Shea & Peterson (1985). Log-transformed morphometric data were statistically analysed with analysis of covariance, using the SYSTAT statistical package (Wilkinson 1987).

Dietary data were obtained by examining stomach contents of six specimens: SAM R2832, R25572, R26160-62, WAM R59753.

Four specimens were maintained alive for some time following collection. The lizards were housed in a vivarium with a heat lamp and fluorescent lighting, both turned on at 0630 h and off at 1930 h,
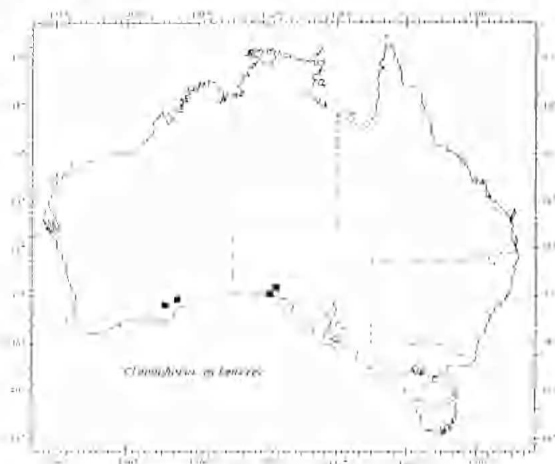
* 69 Alvah Street, St James, Western Australia 6102.
† Department of Veterinary Anatomy, University of Sydney, New South Wales 2006.
‡ School of Biological Sciences, Flinders University, Bedford Park, South Australia 5042.
§ Department of Animal Services, Adelaide University, South Australia 5005.

Fig. 1. Distribution of *C. mckenziei*.

corresponding to the local natural photoperiod at that time. Water, mealworms and chopped fruit were available *ad libitum*. However, one individual (R32266) became emaciated and was euthanased. At 1800 h on 11.xii.1987 (i.e., 54-55 d post capture) the remaining three lizards were placed in a thermal gradient (8-60°C), and allowed to acclimate. Calibrated copper-Constantan thermocouples were placed at least 20 mm into the cloaca and held in position with surgical tape. Cloacal temperatures were electronically recorded every 10 min, for each animal from 1130 h on 12.xii.1987 to 1130 h on 13.xii.1987. Any temperatures taken while lizards were tangled in the thermocouples were excluded from the analysis.

Thermal data were analysed using a one-way ANOVA to test for differences in thermal preferences between individuals. In comparing thermal preferences during scotophase and photophase, data from all individuals were pooled.

Results

Morphology

The South Australian sample (snout-vent length [SVL] 41-76 mm, x̄ = 63.5 mm, n = 11) is similar in morphology and colouration to the Western Australian sample (SVL 31.5-71.5 mm, x̄ = 58.4 mm, n = 7). There are minor, but statistically significant differences between the two (Table 1) in the relationship between tail length (TL) and snout-vent length (slopes, $F_{1,13} = 5.477$, p < 0.05; overall, TL/SVL 215.0-252.9%, x̄ = 233.5%, n = 11 vs 206.3-236.9%, x̄ = 222.5%, n = 6 respectively) and between head depth (HD) and head length (HL) (slopes: $F_{1,0} = 9.900$, p < 0.01; overall, HD/HL 57.7-67.9%, x̄ = 61.4%, n = 11 vs 62.0-67.5%, x̄ = 64.0%, n = 7 respectively), with the eastern juveniles having a longer tail and the eastern adults a more depressed head. It is possible that the apparent long tail on eastern juveniles may be an artefact due to the lack of very small juveniles in the sample.

The affinities of *C. mckenziei* have not previously been adequately defined. Storr (1981) assumed a close affinity with *C. scutulatus* (Stirling & Zeitz, 1893), but provided no argument for this. The *C. mckenziei* material now at hand clearly indicates that this species is very close to *C. scutulatus*. Head, body and limb proportions are similar, the arrangement of spine clusters, rows of enlarged scales and skin folds on the head, neck and body is identical, and most elements of the colour pattern are shared. Both species have the following colouration elements (Fig. 2):

1. a pale vertebral stripe, bordered by
2. a dark paravertebral stripe, bordered laterally by

3. a longitudinal series of pale blotches, coalescing anteriorly and often posteriorly to form an irregular stripe from behind eye, over the ear and upper postauricular spines, to the tail base, where the two stripes often fuse. This element is bordered laterally by

4. an upper lateral zone from below the eye, through the ear, over the forelimb and hindlimb to the proximal part of the tail, bordered ventrally by

5. a broad pale midlateral stripe from axilla to groin, then along hind edge of thigh along the proximal part of the tail, dark margined ventrally;

6. on nape and forebody, a series of dark transverse bars connecting the dark paravertebral stripes and interrupting the pale vertebral stripes;

7. narrow pale caudal rings usually present, overlying other elements of tail pattern;

8. dark ventral markings in males and some females consisting of at least a broad median stripe from chin to gular fold, broadest just rostral to the gular fold, and a rhomboidal to kite-shaped dark breast patch, extending caudally a variable distance, in some cases to the groin. Some specimens of both species have additional dark ventral markings, including streaks and spots laterally on the throat, and dark anterior margins to the thighs (Fig. 3).

Storr (1981) differentiated *C. mckenziei* from *C. scutulatus* by four characters: smaller size, deeper head, fewer subdigital lamellae on the fourth toe and colouration (back blackish brown with whitish vertebral stripe and transverse lines vs pale brown with paired dark brown blotches merging on foreback to form crossbands). The additional material now available supports the size difference (SVL = 31.5-76.5 mm vs 31-115 mm; Storr *et al.* 1983). The smallest male *C. mckenziei* with dilated, wax-filled femoral and preanal pores and turgid testes has SVL = 48 mm (SAM R25572), while a female of the same size (SAM R26890) has well-developed ovaries and oviducts. One female (SAM R2832, SVL = 71.5 mm) is gravid, with three oviducal eggs. However, the remaining three characters employed are non-diagnostic or require qualification.

The purportedly deeper head of *C. mckenziei* is not apparent in our measurements (Table 1), although it is clear from the very much lower values given by Storr (1981) that he used different measurements to obtain a head depth/head length ratio (possibly head depth as defined by Witten [1985]). We have measured head depth at the highest point of the skull, over the parietal eye, and head length from tip of snout to rostral margin of ear. As noted above, the eastern sample of adult *C. mckenziei* had a shallower head than the western sample. A difference of similar magnitude was also present between the eastern sample and *C. scutulatus* (slopes: $F_{1,28} = 8.814$, p < 0.01).
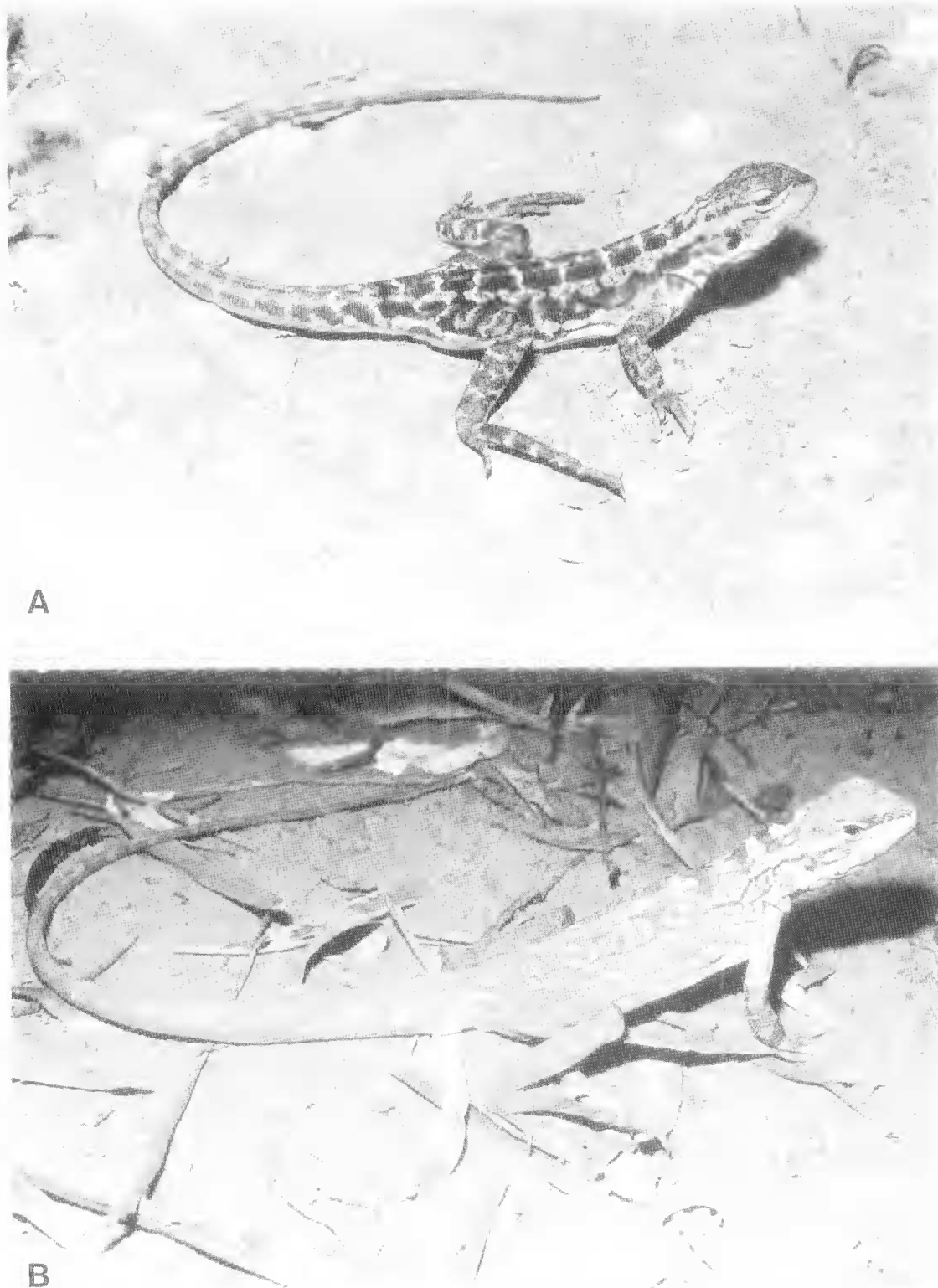
Fig. 2. Dorsolateral views of A. male *C. mckenziei* (15.2 km NE "Colona", SA) and B. male *C. scutulatus* (Hospital Rocks, WA) in life (photographs M. Peterson).

The lower number of subdigital lamellae in *C. mckenziei* is not an absolute difference, and is geographically variable. Western *C. mckenziei* had counts of 25-30 ($\bar{x}$ = 27.4, mode = 27, n = 14) while eastern *C. mckenziei* had 25-32 ($\bar{x}$ = 29.6, mode = 30, n = 18). The *C. scutulatus* sample we examined had 28-41 ($\bar{x}$ = 34.9, n = 80) subdigital lamellae, only 7.5% fewer than 32, although Storr *et al.* (1983) give a range of 31-44. All means are significantly different (pairwise t-tests: eastern *vs* western *C. mckenziei*, t_{30} = 3.36, p < 0.05; western *C. mckenziei vs C. scutulatus*, t_{92} = 10.88, p < 0.005; eastern *C. mckenziei vs C. scutulatus*, t_{96} = 8.33, p < 0.005).

As noted above, the colour pattern is composed of the same elements in each species. The difference noted by Storr (1981) is due to paling of the dark dorsal markings in *C. scutulatus*, particularly the centres of such markings, and enlargement of the pale dorsal spots. The dark crossbands on the foreback of *C. scutulatus* are also present in *C. mckenziei*, though narrower, less contrasting and often fewer.

Sympatry is not yet known between *C. mckenziei* and *C. scutulatus* to confirm a species-level difference, although the two species are known to approach to within 85 km of each other (WAM R91764-65 *vs* R65538, 0.5 km S Buningonia Spring, respectively). However, the lower number of subdigital lamellae in western *C. mckenziei*, which are geographically closest to *C. scutulatus*, together with the much smaller adult size, and consistent evenly dark upper lateral zone (*vs* usually light centred) suggest that *C. mckenziei* is specifically distinct.

Habitat

The two Western Australian localities listed above, and the two South Australian localities 12.6 km NE and 16.2 km NE "Colona" are respectively sites BA2B, BA5, KO2 and KO4 of McKenzie & Robinson (1987), while the localities 0.5 km S and 5 km S Mitcherie Rockhole are sites MI5I and MI2I of Copley & Kemper (1992). From the combination of photographs of the habitat and floristic lists at each locality provided by McKenzie & Robinson (1987) and Copley & Kemper (1992), specimen collection data from both museums and observations by the senior author, it appears that the primary floristic components of the *C. mckenziei*
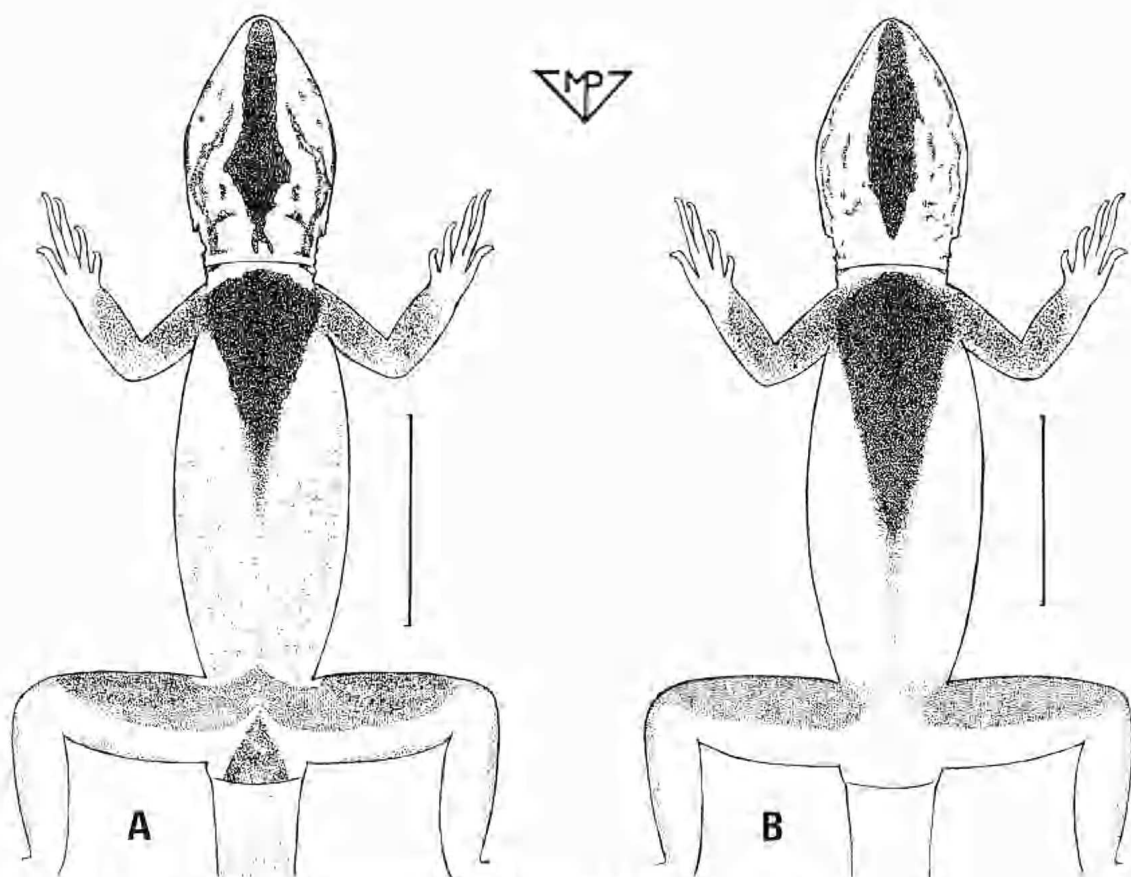

Fig. 3. Typical melanin ventral patterns of A. *C. mckenziei* and B. *C. scutulatus*. Scale bars = 2 cm

habitats are *Eucalyptus oleosa* F.v.M. ex Miq. (giant mallee), *Acacia oswaldii* F.v.M. (umbrella wattle) and *A. papyrocarpa* Benth. (western myall) over a chenopod understorey of *Atriplex vesicaria* Heward ex Benth. (saltbush), *Maireana* spp. (bluebush), *Rhagodia spinescens* R.Br. and *Sclerolaena* spp. The chenopod understorey is common to all localities. The substrate type at sites BA2B, BA5, KO2, KO4 and MI5I is crusting sandy clay loam to loam (McKenzie & Robinson 1987; Copley & Kemper 1992), while the specimen from 15.2 km NE "Colona" was found under a bluebush on a non-crusting sandy substrate, similar to the substrate recorded from site MI2I.

At sites BA2B, BA5, KO2, KO4 and 15.2 km NE "Colona", *C. mckenziei* was sympatric with *C. pictus* (Peters 1866), and at the former three sites it was also sympatric with the agamid *Tympanocryptis lineata* Peters 1864. At site MI2I, it was the only agamid recorded, while at site MI5I, *C. fordi* (Storr 1965) and

Pogona minor (Sternfeld 1919) were also recorded. The latter species was also found at 15.2 km NE "Colona".

Diet

The dominant prey items in all specimens examined were ants, particularly small *Iridomyrmex*, although some larger ants (*Campanotus*, *Melophorus* and other unidentified genera) were present. Other prey items recorded were Hemiptera (single individuals of *Poecilometis* sp. in R22835, R2832, two pentatomids in R2832, and a small unidentified bug in R26162), Coleoptera (one small curculionid prothorax and a large scarab larva in R2832; three unidentified elytra in R25572), Mecoptera (a large abdomen in R2832), Diptera (one small fly wing in R2832), Homoptera (one small wing in R25572), Orthoptera (one small grasshopper head in R25572), Hymenoptera (one small bee head in R25572) and flower parts (R26161).

TABLE 1. *Allometric equations and calculated values for cranial and somatic proportions in* C. mckenziei *(mck),* C. scutulatus *(scu) and* C. cristatus *(cri). Eastern and western samples of* C. mckenziei *are kept separate for tail length and head depth, but pooled elsewhere, as the equations were not significantly different. Values a and b solve the equation* $y = bx^a$, *s.e. is standard error of* a, r^2 = *correlation coefficient,* al. = *direction of significant allometry.* C_{32}, C_{76} *and* C_{105} *are calculated percentage proportions at SVL = 32, 76 and 105 mm (approximate minimum size for all species, maximum size of* C. mckenziei *and approximate large adult size for both* C. scutulatus *and* C. cristatus*).*

	a	s.e.	b	r^2	al.	C_{32}	C_{76}	C_{105}
				AGL/SVL				
mck	1.2128	.0535	.183	.9698	+	.37	.46	—
scu	1.0699	.0284	.323	.9868	+	.41	.44	.45
cri	1.0847	.0381	.295	.9854	+	.40	.43	.44
				TL/SVL				
mck(E)	.9732	.0648	2.606	.9617	0	2.37	2.32	—
mck(W)	1.1662	.0423	1.145	.9948	+	2.04	2.35	
scu	1.1020	.0348	1.586	.9843	+	2.26	2.47	2.55
cri	1.1582	.0282	1.104	.9930	+	1.91	2.19	2.31
				FLL/SVL				
mck	.8350	.0382	.785	.9677	—	.44	.38	—
scu	.9254	.0348	.573	.9739	—	.44	.41	.40
cri	.9706	.0300	.476	.9887	0	.43	.42	.42
				HLL/SVL				
mck	.8714	.0339	1.503	.9763	—	.96	.86	—
scu	.9166	.0311	1.275	.9797	=	.95	.89	.86
cri	.9911	.0196	1.017	.9953	0	.99	.98	.98
				HL/SVL				
mck	.7939	.0458	.530	.9493	—	.26	.22	—
scu	.8563	.0223	.421	.9873	—	.26	.23	.22
cri	.7613	.0179	.631	.9934	—	.28	.22	.21
				HW/HL				
mck	.8719	.0231	1.234	.9889	—	.94	.86	—
scu	.8950	.0175	1.206	.9928	—	.97	.89	.87
cri	.8995	.0193	1.217	.9945	—	.98	.92	.89
				HD/HL				
mck(E)	.7185	.0671	1.286	.9272	—	.71	.58	—
mck(W)	.9809	.0473	.673	.9885	0	.65	.64	
scu	.9312	.0280	.756	.9831	—	.65	.62	.61
cri	.9669	.0287	.726	.9896	0	.68	.66	.66

Behaviour

Two types of circumduction and two types of head-bob were seen. The circumduction types seem to correspond to the challenge wave and submissive wave described by Brattstrom (1971) in *Pogona barbata* (Cuvier 1829). The head-bobs differed in cadence and degree to which the head was moved, aided by extension of the forelimbs. In a dominant male the head was moved a greater distance below and above the normal plane at a faster rate than it was in a subordinate male or two females.

Two captive males were observed in an agonistic display. Upon being placed in the enclosure for acclimation, they head-bobbed and circumducted several times before presenting to each other at a distance of about 15 cm. They were facing in the same direction and continued to head-bob. As the display intensified they coiled their tails loosely and both did several hind-leg push-ups, similar to those described for the *C. decresii* complex by Gibbons (1979). The display ended when one lizard bit the other on the nape. They rolled violently about the cage and then separated.

Temperature preferences

The three *C. mckenziei* studied maintained body temperatures between 11.1°C and 43.4°C ($\bar{x}$ = 34.7°C, σ^2 = 3.41) in a thermal gradient over a 24 h period (Table 2). There were significant differences in thermal preferences between individual lizards (p = 0.04). This may have been due to the low variance of R32267 with respect to the other two individuals. Differences between nighttime and daytime body temperatures were barely significantly different (p = 0.05). However, there was a large difference in voluntary minimum body temperature during photophase (11.1°C) and scotophase (28.7°C). This may reflect greater

activity during the day. Interestingly, the voluntary maximum body temperature (43.4°C) was achieved during the night, indicating that some nocturnal activity occurred.

Discussion

Morphology and relationships

The affinities of *C. mckenziei* and *C. scutulatus* to other taxa remain uncertain. Pianka (1971) stated, without providing evidence, that *C. scutulatus* and *C. cristatus* (Gray 1841) were "obviously rather closely related". Moody (1980)[1] added the *C. caudicinctus* group to the latter complex, diagnosing it on the basis of shape of the medial process of the prearticular bone, limb length, body size, and presence of a nuchal crest and keeled vertebral scale line. Storr (1982), in resurrecting *Ctenophorus*, did not place *C. caudicinctus*, *C. cristatus*, *C. mckenziei* or *C. scutulatus* in any of the species-groups within the genus. Subsequently, Storr *et al.* (1983) placed all four species, together with the *C. reticulatus* species-group of Storr (1966) and *C. decresii* species-group of Houston (1978) in a single expanded *C. decresii* species-group, noting that this was merely an assemblage, and associated *C. mckenziei* and *C. scutulatus* in an undiagnosed informal subgroup, linked by inference (Storr *et al.* 1983: 32) with *C. cristatus*. Witten (1982[2], 1985) placed *C. scutulatus* with the *C. maculatus* group and *C. cristatus* with *C. caudicinctus* in a *C. cristatus* group. Both groups shared dark ventral markings and posterior interscalar femoral and preanal pores. The *C. cristatus* group was differentiated from the *C. maculatus* group by the more widely spaced pores, and smooth (vs usually keeled) ventral scales. The presence of a vertebral scale ridge and a nuchal ridge was considered diagnostic for the *C. cristatus* group, although the presence of both dark ventral pattern and a vertebral scale ridge in *C. scutulatus* was considered primitive within the *C. maculatus* group. A vascular tissue block deep to the vertebral and nuchal ridges, possibly functioning in crest erection, was noted for *C. cristatus* and *C. caudicinctus*, but was not found in the *C. maculatus* group members examined (which did not include *C. scutulatus*). Crest erection was noted for *C. cristatus*, but not for *C. caudicinctus*. We have observed nuchal crest erection in both *C. caudicinctus* (G.M.S.) and *C. scutulatus* (M.P.; Storr *et al.* 1983: Plate 2). However, Witten (1982) considered this vascular tissue block to be plesiomorphic within *Ctenophorus*.

Body, head and limb proportions are similar in *C. cristatus*, *C. mckenziei* and *C. scutulatus* (Table 1) and all share similar male ventral pattern, a nuchal crest, and a vertebral line of enlarged, strongly keeled scales, the latter unlike members of the *C. maculatus* species-group. Consequently, we believe that the affinities of

TABLE 2. *Comparison of thermal preferences among three C. mckenziei run in a thermal gradient. Measurements are in °C.*

Lizard	n	$\bar{x}$	σ^2	Range
R32267	129	35.3	2.43	29.2-39.9
R32268	151	34.4	3.44	11.1-39.0
R32269	138	34.5	4.05	13.0-43.4
Total	418	34.7	3.41	11.1-43.4

$F_{2, 415}$ = 3.2667, p = 0.04.

[1] Moody, S. M. (1980) "Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia). (PhD thesis, University of Michigan).

[2] Witten, G. J. (1982) "Comparative morphology and karyology of the Australian members of the family Agamidae and their phylogenetic implications" (PhD thesis, University of Sydney).

C. mckenziei and *C. scutulatus* are with *C. cristatus*, although it is clear that a more rigorous cladistic analysis of the phylogenetic relationships within the Australian agamid radiation is sorely needed.

Diet

The ant-dominated diet of *C. mckenziei* is similar to that reported for other small *Ctenophorus* species (Pianka 1986; Baverstock 1979; Mitchell 1973). Although *Iridomyrmex* spp. were the most commonly eaten ants, their dominance may simply reflect availability rather than any selection by the lizards (E. Matthews, pers. comm.).

Behaviour

The behaviour reported here for *C. mckenziei* has been observed in other species of Australian agamids. The hind-leg push-up display was thought by Gibbons (1979) to be unique to the *C. decresii* complex. The observations presented here show that this is clearly not the case. Whether this behaviour is homologous in *C. mckenziei* and the *C. decresii* group is unclear.

Thermal preferences

The mean body temperature of *C. mckenziei* reported here is lower than that reported for *C. scutulatus* in a laboratory gradient by Licht *et al.* (1966). It is unclear whether this is a real difference or an artefact of conditions which the animals experience during acclimation or while in the thermal gradient. It is noteworthy that Licht *et al.* (1966) used a thermal gradient in which the minimum temperature available was 25°C, considerably above the voluntary minimum body temperatures experienced by two of the three *C. mckenziei* tested.

While the observation that the voluntary maximum was recorded at night may at first seem unusual in an animal belonging to a group traditionally thought of as diurnal heliotherms, this is not really so. Several species of agamid are known to exhibit some nocturnal activity when thermal conditions allow (Fyfe 1981; Morley & Morley 1985; Bedford 1991; G.R.J., G.M.S., pers. obs.). A constant source of heat in a thermal gradient probably presents as near optimal conditions for nocturnal activity of agamids as possible. However, the low variance exhibited by *C. mckenziei* at night (1.86 *vs* 6.22) indicates that nocturnal activity is limited.

Comparative material examined
(all localities in Western Australia)

C. cristatus: WAM R41827, 2 mi SW Wahlyamoning Rock; R68001-04, R68023-24, 4 km SW Lake Cronin; R68005, R68029, Lake Cronin; R68006, 2.6 km SW Lake Cronin; R68021-22, 5 km SW Lake Cronin; R70707, Frank Hann National Park; R71833, 19.5 km 78° Toomey Hills.

C. scutulatus: SAM R1459a-j, R3024a-b, R4814a-l (syntypes), between Fraser Range and Queen Victoria Springs; WAM R1235, R1761, Laverton; R2841, Gutha; R5306, Wadgingarra; R8170-71, "Yuin"; R9352, Malcolm; R9510, Morowa; R11236, Carnarvon; R12209, Shark Bay; R21865-67, Caron; R48385-89, 40 km N Beacon; R53551, 15 km E Point Sunday; R59605-06, 20 km ENE "Meadow" HS; R86769, 14 km WNW Mallee Hen Rocks.

References

ANONYMOUS (1988) City intrigued to discover that some mice are still rare. *Enplan* (23), 15.

ARMSTRONG, G. P. (1992) Reptiles pp. 163-179. *In* Copley, P. B. & Kemper, C. M. (Eds) "A biological survey of the Yellabinna region South Australia in October 1987" (Dept of Environment & Planning, S. Aust.).

BAVERSTOCK, P. R. (1979) A three year study of the mammals and lizards of Billiat Conservation Park in the Murray mallee, South Australia. *S. Aust. Nat.* **53**, 52-58.

BEDFORD, G. (1991) Additional nocturnal sightings of three species of dragon lizard in nothern Australia. *Herpetofauna* **21**, 30.

BRATTSTROM, B. H. (1971) Social and thermoregulatory behaviour of the bearded dragon, *Amphibolurus barbatus*. *Copeia* **1971**, 484-497.

COPLEY, P. B. & KEMPER, C. M. (1992) "A biological survey of the Yellabinna region South Australia in October 1987" (Dept of Environment & Planning, Adelaide).

CUVIER, G. L. C. F. D. (1829) "Le Règne Animal" (Déterville, Paris).

EHMANN, H. (1992) "Encyclopedia of Australian Animals. Reptiles" (Angus & Robertson, Sydney).

FYFE, G. (1981) Nocturnal sightings of two dragon species. *Herpetofauna* **13**, 34.

GIBBONS, J. R. H. (1979) The hind leg pushup display of the *Amphibolurus decresii* species complex (Lacertilia: Agamidae). *Copeia* **1979**, 29-40.

GRAY, J. E. (1841) Descriptions of some new species and four new genera of reptiles from Western Australia, discovered by John Gould, Esq. *Ann. Mag. Nat. Hist.* **7**, 86-91.

HOUSTON, T. F. (1978) "Dragon Lizards and Goannas of South Australia" (South Australian Museum, Adelaide).

LICHT, P., DAWSON, W. R., SHOEMAKER, V. H. & MAIN, A. R. (1966) Observations on the thermal relations of Western Australian lizards. *Copeia* **1966**, 97-110.

MCKENZIE, N. L., ROLFE, J. K. & CARTER, D. (1987) Reptiles pp. 179-210. *In* McKenzie, N. L. & Robinson, A. C. (Eds) "A biological survey of the Nullarbor region South and Western Australia in 1984." (South Australian Department of Environment and Planning, Western Australian Department of Conservation and Land Management and Australian National Parks and Wildlife Service).

_____ & ROBINSON, A. C. (1987) *Ibid.*

MITCHELL, F. J. (1973) Studies on the ecology of the agamid lizard *Amphibolurus maculosus* (Mitchell). *Trans. R. Soc. S. Aust.* **97**, 47-76.

MORLEY, T. P. & MORLEY, P. T. (1985) An inventory of the reptiles of Danggali Conservation Park. *Herpetofauna* **15**, 32-36.

PETERS, W. (1864) Übersicht der von Hrn. Richard Schomburgk an das zoologische Museum eingesandten Amphibien, aus Buchsfelde bei Adelaide in Südaustralien. *Mber. K. Preuss. Akad. Wiss. Berlin* **1863**, 228-236.

PETERS, W. (1866) Eine Mitteilung über neue Amphibien (*Amphibolurus, Lygosoma, Cyclodus, Masticophis, Crotaphopeltis*) und Fische (*Diagramma: Hapalogenys*) des Kgl. zoologischen Museums. *Ibid.* **1866**, 86-96.

PIANKA, E. R. (1971) Notes on the biology of *Amphibolurus cristatus* and *Amphibolurus scutulatus. West. Aust. Nat.* **12**, 36-41.

_____ (1986) "Ecology and natural history of desert lizards. Analyses of the ecological niche and community structure." (Princeton University Press, Princeton, New Jersey).

SCHWANER, T. D. & TYLER, M. J. (1985) Reptiles and amphibians pp. 56-67. *In* Aslin, H. J. (Ed.) "A list of the vertebrates of South Australia".

SHEA, G. M. & PETERSON, M. (1985) The Blue Mountains Water Skink, *Sphenomorphus leuraensis;* a redescription, with notes on its natural history. *Proc. Linn. Soc. N.S.W.* **108**, 141-148.

STERNFELD, R. (1919) Neue Schlangen und Echsen aus Zentralaustralien. *Senckenbergiana* **1**, 76-83.

STIRLING, E. C. & ZEITZ, A. (1893) Vertebrata. *Trans. R. Soc, S. Aust.* **16**, 154-176.

STORR, G. M. (1965) The *Amphibolurus maculatus* species-group (Lacertilia: Agamidae) in Western Australia. *J. R. Soc, West. Aust.* **48**, 45-54.

_____ (1966) The *Amphibolurus reticulatus* species-group (Lacertilia: Agamidae) in Western Australia. *Ibid.* **49**, 17-25.

_____ (1981) Three new agamid lizards from Western Australia. *Rec. West. Aust. Mus.* **8**, 599-607.

_____ (1982) Revision of the Bearded Dragons (Lacertilia: Agamidae) of Western Australia with notes on the dismemberment of the genus *Amphibolurus. Ibid.* **10**, 199-214.

_____, SMITH, L. A. & JOHNSTONE, R. E. (1983) "Lizards of Western Australia. II. Dragons and Monitors." (Western Australian Museum, Perth).

WILKINSON, L. (1987) SYSTAT: the system for statistics. (SYSTAT Inc., Evanston).

WILSON, S. K. & KNOWLES, D. G. (1988) "Australia's Reptiles. A photographic reference to the terrestrial reptiles of Australia." (Collins, Sydney).

WITTEN, G. J. (1985) Relative growth in Australian agamid lizards: adaptation and evolution. *Aust. J. Zool.* **33**, 349-362.